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Extramuscular myofascial force transmission within the rat anterior tibial compartment: proximo-distal differences in muscle force

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ABSTRACT

Intramuscular connective tissues are continuous to extramuscular connective tissues. If force is transmitted there, differences should be present between force at proximal and distal attachments of muscles. Extensor digitorum longus (EDL), tibialis anterior (TA), and extensor hallucis longus muscles (EHL) were excited simultaneously and maximally. Only EDL length was changed, exclusively by moving the position of its proximal tendon. Distal force exerted by TA + EHL complex was not affected significantly. Proximal and distal EDL isometric force were not equal for most EDL lengths: $F_{prox} - F_{dist}$ ranged from 0 to ≈+22.7% of F_{prox} at higher lengths and from 0 to ≈–24.5% at the lowest lengths. It is concluded that extramuscular connections transmit force from muscle. Significant proximo-distal differences of EDL force remained after repeated measurements, regardless of length order, although their length dependence was altered. Measurements of both proximal and distal EDL force were highly reproducible, if EDL did not attain higher lengths than target length. After being active at high lengths, proximal and distal length–force curves were altered at low lengths but not for the highest length range. Extensor digitorum longus length–active force hysteresis was present for proximal as well as distal EDL measurements with increasing and decreasing isometric length order. Further isolating EDL removed the proximo-distal difference for active EDL force. However a decreased difference for passive EDL force remained, which was ascribed to remaining extramuscular connective tissue linkages. It is concluded that extramuscular myofascial force transmission is an important feature of muscle that is not isolated from its surrounding tissues.

Keywords anterior tibial compartment, anterior tibial muscle, connective tissue, dissection, extensor digitorum longus muscle, extensor halucis longus muscle, fasciotomy, length–force characteristics, myofascial force transmission, proximo-distal force difference, rat.

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In addition to myotendinous force transmission, a second pathway has been shown to exist, that uses the muscle's cytoskeletal lattice and trans-sarcolemmal molecules as well as basal lamina connecting molecules to transmit force onto connective tissue. Such a mechanism of force transmission was shown to be active in experiments on single isolated muscle fibres (Ramsey & Street 1940) and small fascicles (Street 1983, Street & Ramsey 1965). Its activity has also been inferred for non-spanning fibred muscle. This muscle, containing fibres that do not necessarily span the distance between proximal and distal muscle fibre attachment areas of a muscle on aponeuroses or bone, but end somewhere in a fascicle that itself is attached at both ends. It is evident that for such fibres force must be transmitted to neighbouring tissues at least at one fibre end (Loeb *et al.* 1987, Trotter 1990, 1991, 1993, Scott *et al.* 1992, Trotter & Purslow 1992, Trotter *et al.* 1992, 1995, Eldred *et al.* 1993a,b, Hijikata *et al.* 1993, Hijikata & Ishikawa 1997, Monti *et al.* 1999). With few exceptions (i.e. Eldred *et al.* 1993a, b, Monti *et al.* 1999), these authors generally view transmission of force as a process between adjacent muscle fibres, which will eventually lead to myotendinous

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force transmission in the muscle fibre to which the force is transmitted.

Recently, we reported evidence that force transmission at the periphery of the muscle fibre also plays an important role within muscles, isolated *in situ*, of which muscle fibres do span the full distance between proximal and distal muscle fibres attachment areas of a muscle on aponeuroses or bone (Huijing *et al.* 1998, Huijing 1999a). This means that the mechanism is not limited to tapering non-spanning muscle fibres, but may be regarded as a very general mechanism of skeletal muscle.

In addition, we proposed that force, at the muscle fibre's perimeter, is predominantly further transmitted onto the intramuscular connective tissue network. Therefore, this mechanism has been named myofascial force transmission (e.g. Huijing *et al.* 1998, Huijing 1999a). If the intramuscular connective tissue is indeed a major path for force transmission, the question needs to be addressed: Where it will force be transmitted to from that network?

It was hypothesised that myofascial force transmission may also play a role extra-muscularly (Huijing 1999a), i.e. transmission to connective tissues outside the muscle. Some recent explorative experimental work (Huijing 1999a) yielded at least some indications that this concept may be entertained and should be studied systematically. It was argued that part of the muscular force is transmitted onto limb compartmental connective tissues and thus not fully onto a muscle's own tendon(s). If such an effect takes place, it means that force exerted at the origin tendon and the insertion tendon of a muscle should not necessarily be equal, if the muscle is maintained within its natural *in vivo* surroundings.

Therefore, the purpose of the present study was threefold: (1) to perform a systematic study regarding the existence of any proximo-distal differences in force exerted via the tendons of a muscle surrounded by the connective tissues and other muscles of its compartment, and its dependence on muscle-tendon complex length, and (2) to study if any such difference is maintained during different repeated measurements of length–force characteristics, and (3) to study the effects of isolating the muscle from surrounding tissues within the compartment.

MATERIALS AND METHODS

Surgical and experimental procedures were in strict agreement with the guidelines and regulations concerning animal welfare and experimentation set forth by Dutch law, and were approved by a Committee on Animal Experimentation at the Vrije Universiteit, Amsterdam. Immediately after all experiments, double-sided pneumothorax was performed and animals were killed with an overdose of pentabarbital.

Surgical procedure and preparation for experiment

Surgery. Male Wistar rats ($n = 10$, mean ± SD of body mass 317 g ± 22.0) were anaesthetized by intraperitoneally injecting a urethane solution (initial dose 1.2 mg/100 g body mass). Supplementary doses of the anaesthetic agent (0.62 mg) were injected intraperitoneally (maximally three times), if necessary to maintain deep anaesthesia. The animals were placed on a heated water pad (37 °C) during surgery and experimentation.

In the rat, connective tissue associated with the biceps muscle covers the anterior compartment in order to reach a very long insertion along the tibia. The left anterior crural compartment of the left leg was exposed by removing the skin, parts of the crural fascia and the biceps femoris muscle. The femoral compartments were opened in order to: (1) attach a clamp to the femur for later fixation of the animal; (2) reach the proximal tendon of m. extensor digitorum longus (EDL). This proximal tendon was cut as proximally as possible and sutured in a loop (Ethicon Perma-hand Seide 5/0 C3; Johnson & Johnson, Brussels, Belgium). To this tendon loop, a looped Kevlar thread (4% elongation at a break load of 800 N) was sutured; (3) dissect the sciatic nerve and cut it as proximally as possible. The sural, tibial and articular branches of the sciatic nerve were cut, so that by stimulating the sciatic nerve during the experiment, the full motor segment of the common peroneal nerve would be excited exclusively.

Apart from the preparatory intervention of removal of the biceps femoris muscle, the proximal segment of the anterior crural compartment was not interfered with, to maintain physiological relations of intra- and extramuscular connective tissue as much as possible. The very distal part of the anterior tibial compartment had to be opened to reach the distal tendons of EDL and of the extensor hallucis longus (EHL) and tibialis anterior (TA) muscles. With the knee joint at 90° and the angle between the foot plate and the tibia at 90° (referred to as reference position), two sets of distal tendons were tied together: (1) the four distal tendons of EDL. (2) The distal EHL tendon was tied to the distal tendon of TA. Matching markers were placed on the distal tendons of EDL and of TA and EHL, as well as on a fixed location on the lower leg. Subsequently, the distal EDL and the distal TA + EHL tendon complexes were cut as distally as possible and removed from their retinaculae near the ankle joint (transverse crural ligament and cruciate ligament). Each of the two groups of distal tendons were looped and sutured (polyester thread) in this shape. Looped Kevlar threads (4% elongation at a break load of 800 N) were tied (three knots) to the distal tendon loops.

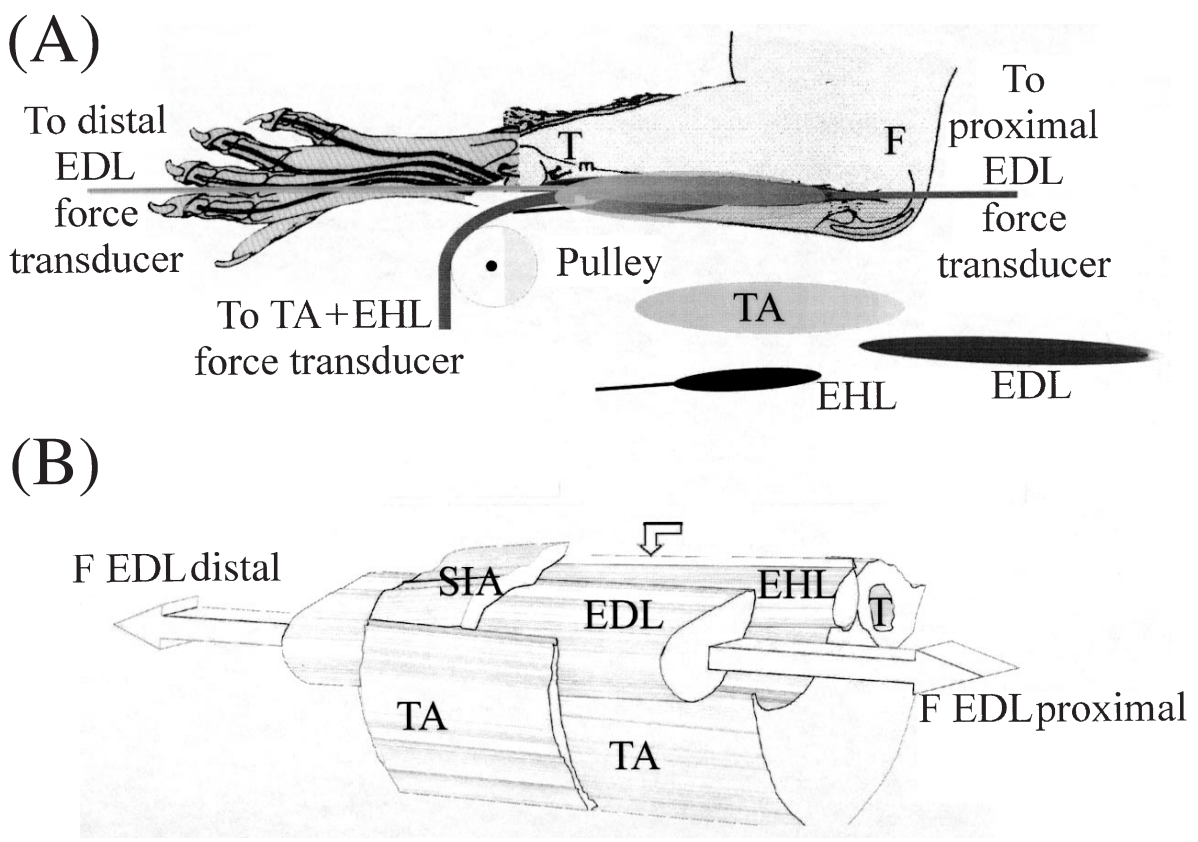

Figure 1 Schematic representation of the experimental set up and anterior tibial compartment. (a) The foot was brought into extreme plantar flexion to create room for passing of distal extensor digitorum longus (EDL) tendons and their attachments. Proximal and grouped distal EDL tendons were attached to their respective force transducers. Distal tendons of tibialis anterior muscle (TA) and extensor hallucis longus muscle (EHL) were tied together (TA + EHL) and via a low friction pulley attached to a force transducer that, for reasons of space, was placed perpendicular to the other two force transducers. (b) The anterior tibial compartment is delimited by (1) the anterior intermuscular septum (SIA), (2) a part of the interosseal membrane (MI). MI is attached to the tibia (T) and the fibula (not shown). (3) The tibial lateral aspect and (4) TA muscle and its surrounding connective tissue. In fact TA completely envelops the other two muscles.

The left foot of the rat was attached firmly to a plastic foot plate using Kevlar thread.

Mounting the animal in the experimental apparatus. After the rat was mounted in the experimental apparatus, the femur was secured by means of the metal clamp. The plate with the left foot attached was manipulated such that the ankle was in extreme plantar flexion to make room for passage of distal tendon groups and their attached Kevlar threads (Fig. 1), after which the plate was firmly attached to the experimental apparatus. The (TA + EHL) complex was brought to a length corresponding to length at reference position – 5 mm, i.e. relatively low length, yielding a summed active force of approximately 0.5 N. The EDL distal tendon group was set at a length corresponding to reference position.

All Kevlar threads were connected to force transducers (Hottinger Baldwin, maximal output error <0.1%, compliance 0.0048 mm N^{-1}). To check alignment of EDL proximal and distal tendons and their Kevlar threads, visual inspection was performed and images collected for post-experimental checks of fulfilment of this criterion (e.g. Fig. 4a).

The position of the force transducers was manipulated to obtain an orthogonal orientation with respect to the Kevlar threads.

The severed end of the sciatic nerve was placed on a bipolar stimulation electrode.

Interventions for visualization of connective tissue. In one additional animal, visualization of connective tissue within the anterior tibial compartment was obtained after full compartmental fasciotomy. In this condition, first the TA muscle was loaded by attaching weights to pull the muscle away from its normal position in anterior and lateral directions. Increasing the pulling force destroyed some connections between TA and its surroundings while exposing other ones. Subsequently TA and EHL were removed in such a way, as to isolate EDL in a way comparable with that of the experiment. This means that isolation was not complete, but a proximal remnant of TA remained, as well as a major

neurovascular tract and its connective tissue. Digital images were taken using a VGA progressive Scan CCD camera with 16 mm lens and treated using an image handling system (version 6.0, Optimas Corp., Bothell, Washington, USA).

Experimental procedure and data collection

In order to make sure that any differences in force transducers and their calibration, prior to the experiment introduced no artefact, the two force transducers to be used for the measurement of EDL forces were connected to each other using a compliant spring. The output was recorded with the same measurement system (i.e. amplifiers, A–D converters) used in the animal experiment. It is concluded that any major difference in force (>1.36%) at these transducers cannot be ascribed to the measurement system used. In addition to that, the locations of these force transducers with respect to EDL were exchanged in half of the experiments.

During the experiments, ambient temperature was kept constant at 22° ± 0.5 °C and air humidity was kept at 80 ± 2% by a computer-controlled air conditioning system (Holland Heating) creating a down flow of air onto the experimental table. The surface of the crural compartment was rinsed regularly with saline to prevent fluid loss.

Tibialis anterior, EHL and EDL muscles (all innervated via the deep peroneal nerve), were excited simultaneously. This was done by stimulating the, distal end of the severed, sciatic nerve supra-maximally, using a pair of silver electrodes connected to a constant current source (square pulse width 100 μs, pulse train 400 ms, 100 Hz). In the preparatory phase of each experiment current was increased in small steps until no further increase in force was attained. In this condition, currents of approximately 3 mA were necessary. The constant current mode of the stimulator delivers the set amplitude of current, even if changes of nerve impedance should occur during the experiment, thereby helping to maintain maximal excitation of the nerve during the course of the experiment. To prevent drying of the nerve, the exposed part was covered with isotonic saline saturated paper tissue, which itself was covered by a thin layer of latex.

The positions of distal tendons of the TA + EHL complex were kept constant during the experiment. As the origins of these muscles were not treated in any way the length of this complex was constant during experiments.

Initial determination of length–force curves. Specific care had been taken that experimental muscles did not attain high length prior to this part of the experiment. Isometric tetanic EDL force was measured at various lengths with simultaneous measurements of force of the TA + EHL complex, while at constant complex length. EDL length changes were imposed by moving the proximal force transducer (1 mm increments, as determined on a vernier mechanism read to the nearest tenth of a mm) in between contractions. Distal tendons were kept at reference position. Length–force data were obtained starting from a proximal position at which the knot at the proximal EDL tendon just did not touch the entrance of anterior tibial compartment. These proximal and distal positions of EDL correspond to a minimal EDL length of several mm over active slack length (i.e. the lowest muscle length at which active muscle force approaches zero). Following each contraction the muscles were allowed to recover for 2 min, to minimize any effects of fatigue and potentiation. For EDL, recovery was allowed to occur near minimal EDL length.

After stretching the muscle to the desired length, two twitches were evoked (200 ms apart). Passive force was determined approximately 600 ms after the second twitch. Almost immediately after that, the muscle was excited tetanically. During the tetanic plateau (i.e. 275 ms after evoking tetanic stimulation) total isometric muscle force was determined.

Subsequent procedures. After initial determination of length–force curves, the experimental animals were assigned to one of the two groups ($n = 5$ each):

(B1) The first group was used to assess reproducibility of length–force measurements, as well as effects of length history on length–force characteristics. For that purpose the procedure of determination of the initial length–force curves was repeated several times with the following modifications:

(i) Higher muscle lengths were imposed progressively (1 mm increments) but isometric contractions at any given length was repeated three times. The 2 min recovery interval at low length after each isometric contraction was maintained also in this condition. A test contraction was performed at initial optimum length to assess any acute effects of the highest lengths;
(ii) Subsequently length–force curves were determined again using the initial procedure. The 2 min recovery interval at low length after each isometric contraction was maintained also in this condition. A test contraction was performed at initial optimum length to assess any acute effects of the highest lengths;
(iii) After 2 min recovery at low length, the length–force curves were determined in reverse order, i.e. starting at the highest length followed by 1 mm decrements. A test contraction was performed at

initial optimum length to assess any acute effects of this particular length history; and
(iv) After 2 min recovery at low length, length–force curves were determined again applying the initial procedure (increasing lengths).

(B2) After removing most of the TA + EHL complex (i.e. isolation of EDL) the initial procedure was repeated. Removal of this complex involved the following interventions:

(i) Extensive fasciotomy over the full lateral aspect of the anterior tibial compartment;
(ii) Dissecting EDL free of the TA + EHL complex and all other tissues of the compartment, with the exception of leaving extramuscular connective tissue of the EDL neuro-vascular tract (Huijing & Baan 2001) intact; and
(iii) cutting of TA and EHL muscles.

All force signals were acquired using an A/D converter (sample frequency 1000 Hz, resolution of force 0.01 N) and recorded on a microcomputer. A special purpose microcomputer controlled the timing of events related to stimulus generation as well as A/D-conversion.

Treatment of data. The individual length–force data sets for passive muscle force and muscle length were fitted with an exponential curve (Eqn 1), using a least squares criterion.

$$y = e^{a1+a2\cdot x} \quad (1)$$

where y represents passive muscle force, x represents passive muscle-tendon complex length (i.e. deviation from minimal length, Δl) and a_1 and a_2 are coefficients determined in the fitting process. Active muscle force (F_{ma}) was estimated by subtracting passive force calculated according to Equation 1 for the appropriate active muscle tendon complex length from the total force exerted by the muscle at that length.

Data for active EDL force (F_{ma}) in relation to changes of active muscle-tendon complex length (Δl_{oi}) were fitted using a polynomial:

$$y = b_0 + b_1\cdot x + b_2\cdot x^2 + \cdots + b_n\cdot x^n \quad (2)$$

where y represents active muscle force F_{ma}, $\times$ represents length of the active muscle-tendon complex, n represents the order of the polynomial and b_0, $b_1 \cdots b_n$ are coefficients determined in the fitting process. The fitting started with a first order polynomial and the power was increased up to and including the sixth order. Polynomials that best described the experimental data were selected (see below). These polynomials were used for three purposes:

(i) Averaging of data and calculation of standard errors;
(ii) Determining EDL optimal force; and
(iii) Optimum length. For each individual muscle optimal muscle force (F_{mao}) is defined as the maximum of the fitted polynomial for active muscle force and optimum muscle-tendon complex length is defined as the corresponding active length.

Individual data for muscle-tendon complex length were expressed as deviations from minimal EDL length.

Statistics

In the fitting procedure one-way analysis of variance (ANOVA) (Neter *et al.* 1990) was used to select the lowest order of the polynomials that still added a significant improvement of the description of changes of muscle–tendon complex length and muscle force data for EDL.

Two-way ANOVA for repeated measurements (factors: muscle length and location of EDL force measurement) was performed to test for effects on muscle length–force characteristics. To test for differences in proximal and distal optimum length as well as for EDL length effects on TA + EHL force, one way ANOVA was performed. If significant effects were found, post-hoc tests were performed using the Bonferroni procedure for multiple paired comparisons, to further locate significant differences. Any differences at $P \leq 0.05$ were considered significant.

RESULTS

Proximal and distal EDL forces are for the most part not identical

A number of muscle–tendon complex lengths were obtained by moving exclusively the proximal EDL force transducer to new target positions. Isometric EDL force (in passive and active conditions) was measured simultaneously at proximal as well as distal force transducers. Figure 2 shows superimposed examples of force time traces at three lengths. Note the length dependent differences of variable magnitude between EDL forces measured at distal and proximal tendons.

Also note that the time course of the tetanic contraction is length dependent and may differ for simultaneously measured forces at EDL proximal and distal tendons (e.g. the low length trace).

Length–force characteristics

Active. The effects of increasing EDL length, obtained by proximal lengthening of the muscle, on both proximal and distal isometric force are shown in Fig. 3.

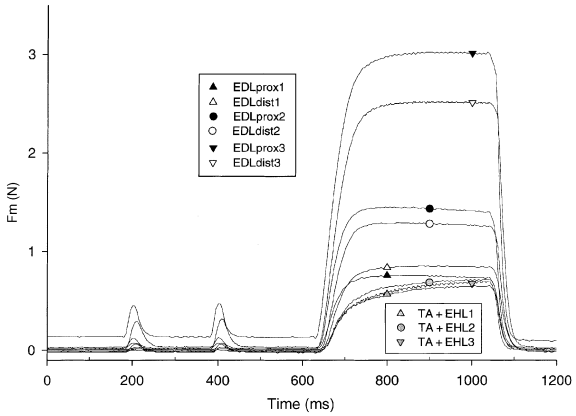

Figure 2 Typical examples of force time traces as measured at extensor digitorum longus (EDL) proximal as well as distal tendons and at the distal tendon of the tibialis anterior muscle (TA) + extensor hallucis longus muscle (EHL) complex. Traces recorded for an individual muscle at three lengths of EDL (1: Δl_{oi} EDL ≈0 mm; 2: Δl_{oi} EDL ≈2 mm and 3: Δl_{oi} EDL ≈8 mm) are superimposed. Note the length dependence of the sign as well as of the magnitude of the difference between proximal and distal EDL force. Also note that the pattern of the proximal and distal force EDL force may differ (e.g. for lowest length shown).

Significant differences as well as significant interactions (between the factors length and location within the muscle) were found for both active and passive EDL length–force characteristics, as determined proximally and distally. The ascending limb of the active EDL length–distal force curve is considerably less steep than that of the EDL length–proximal force curve (Fig. 3a), but starts at a significantly higher force at minimal EDL length, and attains significantly lower values at higher EDL lengths. Optimum lengths of the length–force curves determined distally and proximally were not significantly different. These effects cause both curves to cross (i.e. proximal force equals distal force at Δl≈0.7 mm). Therefore the difference in force between proximal and distal force transducers is seen at any experimental length, except for this 'crossover length'. The magnitude of this significant proximo-distal difference in EDL force (i.e. $F_{prox} - F_{dist}$) is substantial and highly length dependent (changing from 0 to ≈+22.7% of the proximal force at higher lengths and rapidly increasing from 0 to ≈ –24.5% at lower lengths).

Passive. The passive EDL length–force curve measured proximally (Fig. 3a) has relatively high slopes near optimum length. Significant effects as well as interactions were found for passive length–force curves. At most EDL lengths, except the very lowest ones studied, passive distal EDL force was significantly lower than passive EDL force measured proximally. At the any given EDL length also the slope of the length–force curve determined distally was lower than that of the proximal curve.

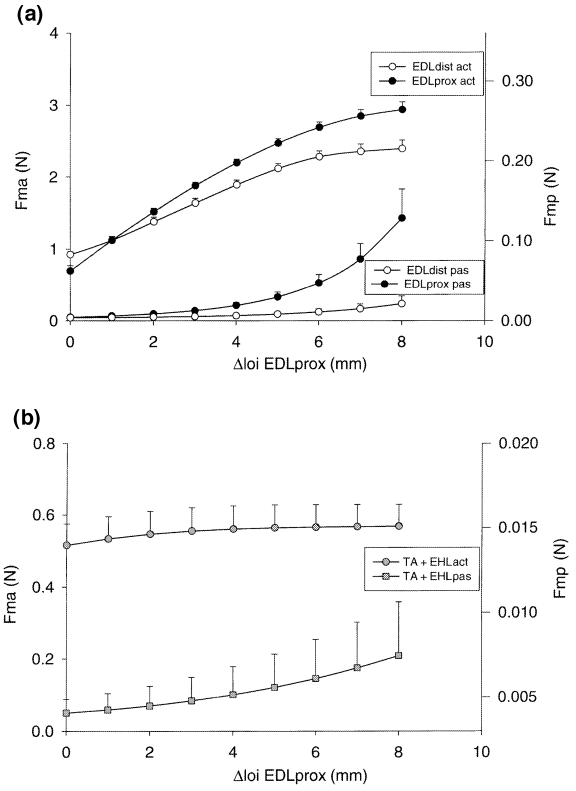

Figure 3 Force exerted by muscles located with the anterior tibial compartment with intact surrounding connective tissues. (a) Active and passive length–force characteristics of extensor digitorum longus (EDL) as measured at its proximal and distal tendons. (b) Active distal forces and passive distal tibialis anterior muscle (TA) + extensor hallucis longus muscle (EHL) forces exerted at constant low length. Force exerted by this complex is also expressed as a function of EDL length (Δl_{oi} EDL, i.e. deviations from a minimal length, see methods, as obtained by proximal lengthening). The F_{ma} and F_{mp} represent active and passive force, respectively. Note that different axes are shown for active (left vertical axis) and passive forces (right vertical axis), with quite different scaling factors. Mean results and standard errors of the mean ($n = 10$) are shown. 'act' and 'pas' indicate curves for active and passive force, respectively.

These combined results for active and passive forces and particularly their differences between proximal and distal locations represent a clear proof that, with most of the anterior tibial compartment intact, a pathway must exist for force to be transmitted to and from the EDL muscle to structures other than its proximal and distal tendons. The additional active and passive forces have to be borne also by the two pathways within the proximal segment of EDL the intramuscular connective force and sarcomeres in series, which have to attain higher lengths (than in the distal segment) to be able to do that.

Distal force in the complex of tibialis anterior and extensor hallucis longus muscles. It is conceivable that (part of) the difference between proximal and distal EDL forces could be transmitted directly (i.e. by intermuscular

connections) onto the TA + EHL muscle complex. The examples of force time trace for this muscle complex (Fig. 2) indicates small differences as a function of EDL length. However, despite simultaneous EDL length dependent differences in force exerted at proximal and distal EDL tendons, no significant changes could be shown for the active forces of TA + EHL muscles (Fig. 3b). Therefore there is no unequivocal evidence for intermuscular myofascial force transmission. This can be interpreted in two ways:

(i) Either no force is transmitted intermuscularly, which would mean that extramuscular myofascial force transmission is the sole source of the proximo-distal difference in EDL force.
(ii) There is no net force transmission from EDL to the TA + EHL complex (i.e. equal force is transmitted in opposite directions between these muscles in different locations). In any case, it is concluded that the present work yields no unequivocal evidence supporting the concept of direct intermuscular force transmission.

Visualization of connections between extensor digitorum longus and the tibialis anterior–extensor hallucis longus complex and surroundings. Figure 4a shows an example of the anterior tibial compartment as manipulated during the experiment. Distally, within the anterior tibial compartment, and proximally, within the femoral compartments, tendons of EDL protrude. At the level of the EDL muscle belly, EDL is completely surrounded by TA. Also EHL cannot be seen. The alignment of EDL, is judged from the alignment (see line superimposed on the image) of its proximal and distal tendons and their Kevlar connections to the force transducers.

A visualisation of any extra- and inter-muscular connections and some of their effects is possible, only after full compartmental fasciotomy and (artificial) displacement of muscles from their original position (Fig. 4b–e). By applying external force exclusively to TA via two ligatures in its muscle belly (black silk and white arrows in Fig. 4b), EDL is pulled down as well (compare Figs 4a,b) indicating that force is exerted on that muscle via TA. Although force is not exerted directly on EDL, its is pulled downward via exposed connections between TA and EDL. Note that at the middle of the muscle belly but also at the tendons EDL is displaced considerably with respect to the original line of pull. This action also visualizes some of the very short connections between these muscles at their interface. However it should be realized that in this demonstration such connections are loaded predominantly under considerable tensile stress and break easily, whereas, *in vivo*, shear stress is expected to be the major load and stiffness and material strength under such load is expected to be higher.

After subsequently applying downward directed force directly on EDL (Fig. 4c), the muscle rotated in lateral direction. This means that in addition to the downward forces a third force is holding back EDL. These forces created a couple yielding the rotation. This rotation exposes connective tissue that links EDL, but also TA and EHL to other tissues of the compartment.

The origin of this additional force was a complex sheet-like connective tissue structure entering the medial aspect of the EDL muscle belly (Fig. 4d). This sheet also contains major neurovascular tracts of the compartment and is connected to other compartmental tissue, such as the anterior intermuscular septum as well as sheets entering TA and EHL.

Combining physiological and morphological results, it is concluded that extramuscular myofascial force transmission did occur via elements of connective tissue of the tibial anterior compartment.

Reproducibility of length–force measurements and EDL proximo-distal force difference at specific lengths

Active force. Figure 5 shows that if force is measured repetitively at a target length, without muscles attaining higher lengths than the target length, EDL length–active force characteristics are highly reproducible for muscles with 2 min rest at low length between contractions. No significant effects could be shown for either proximal or distal forces. Note that also at higher lengths force is measured reproducibly.

As a consequence of the reproducibility, also EDL proximo-distal active force difference was present and the length dependence of its magnitude and sign were unaltered in each repetition.

Passive force. In these experiments passive force levels reached significantly higher levels (approximately 4x as high) at the proximal than at distal EDL tendons (compare Fig. 5a, b). This must be related to the fact that EDL length was changed exclusively at the proximal tendon. It seems that elements responsible for passive proximal force EDL (e.g. sarcomeres and endomysium) attain higher lengths than distal elements.

Significant differences for repetitive curves were found for neither proximal nor distal EDL length–passive force curves.

It is concluded that length–force measurements are quite reproducible for muscle that has not been active at higher lengths than its target length.

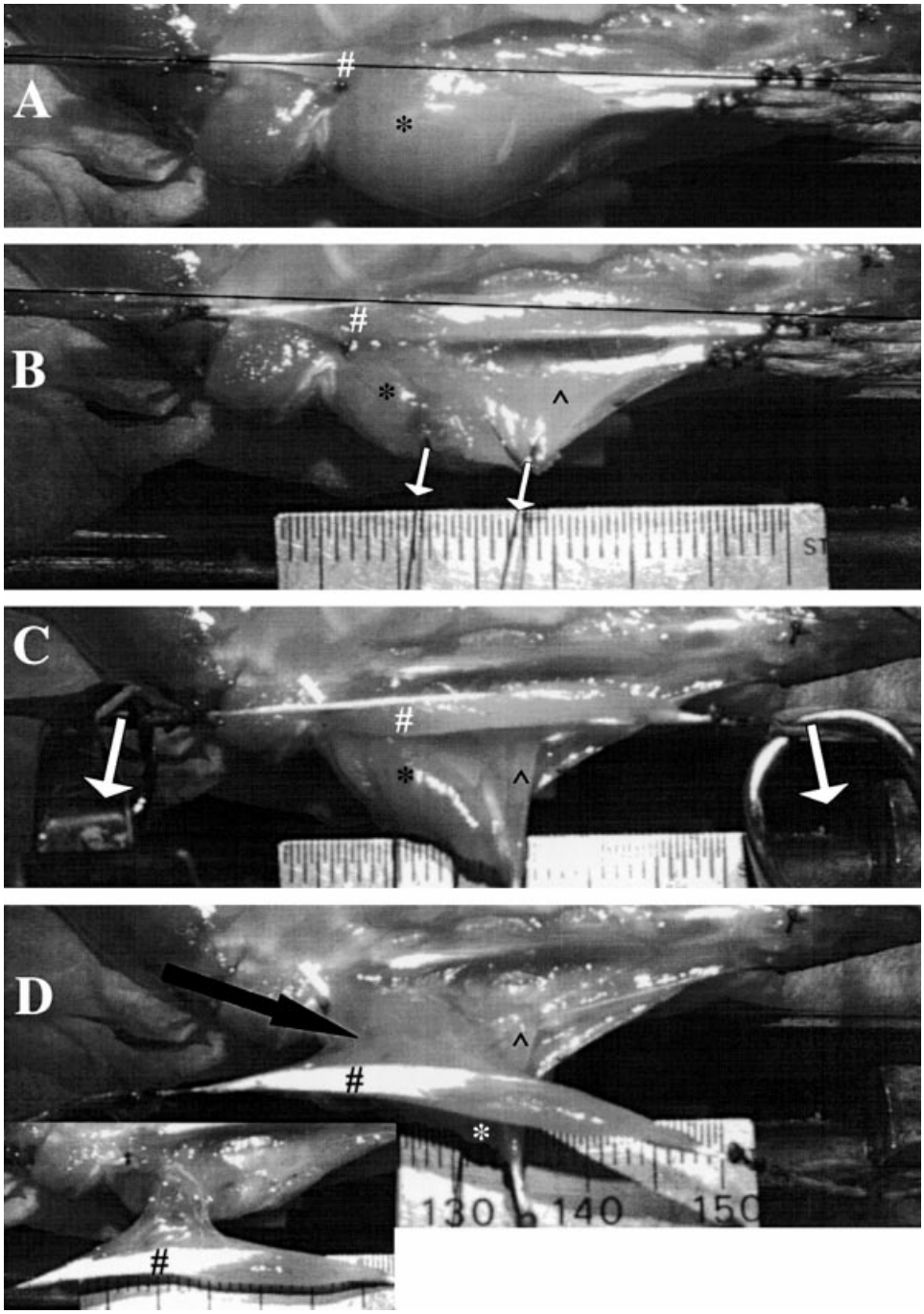

Figure 4 Muscles and other elements of the anterior tibial compartment. Manipulation performed to illustrate connections between them. (A) The initial condition of all experiments. The drawn line indicates the line of pull of extensor digitorum longus (EDL). (B) After full compartmental fasciotomy, and exertion of a downward force is on tibialis anterior muscle (TA) (via two black silk ligatures in its muscle belly, white arrows). For reference, the line of panel A, is placed also in panel B at the identical position. After progressively breaking intermuscular TA–EDL connections, the distal complex of tendons of TA + EHL was fixed in the position shown. (C) Subsequently a downward force (white arrows) was exerted at the proximal and distal Kevlar threads, which form the connections to the EDL force transducers. EDL was pulled down and rotated approximately 90° in lateral direction. (D) The connective tissue sheet (black arrow), exposed after rotation, connects the muscles to the compartment walls (tibia, part of interosseal membrane and anterior intermuscular septum) but also carries major blood vessels and nerves of the compartment. (E) Inset of D. An example of the part of the neurovascular tract to EDL that remains after dissection of EDL from its surroundings. The following symbols indicate the following muscle bellies, respectively: # – EDL, * – TA and ^ – EHL. The smallest division of the ruler shown represents 0.5 mm. The ruler shown in panel B is also valid for panel A.

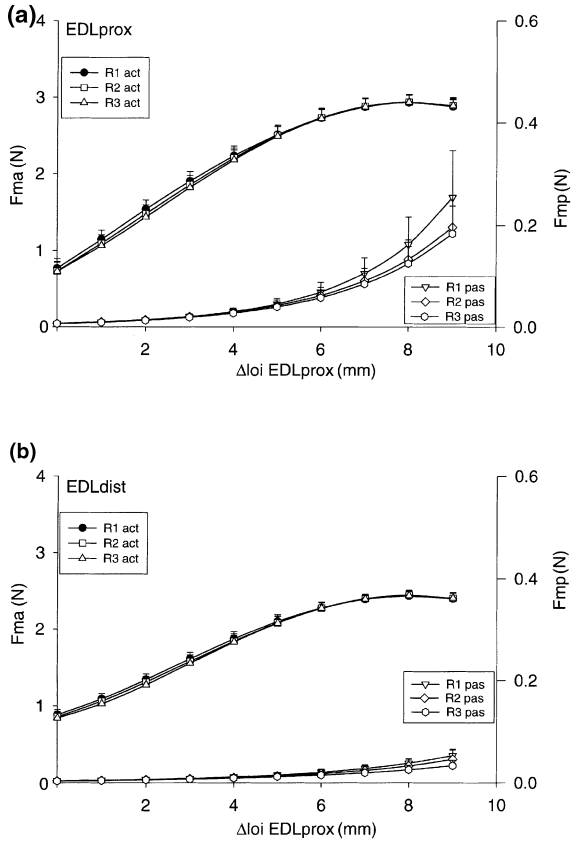

Figure 5 Reproducibility of repeated length–force measurements for EDL. The EDL length was increased by proximal lengthening and brought to each target length three times at two minute intervals. Target lengths were studied in increasing length order. (a) Active and passive EDL length–force characteristics as measured at its proximal tendon. (b) Active and passive EDL length–force characteristics as measured at its distal tendon. F_{ma} and F_{mp} represent active and passive force, respectively. Note that different axes are shown for active (left vertical axis) and passive forces (right vertical axis), with quite different scaling factors. Mean results and standard errors of the mean ($n = 5$) are shown. 'act' and 'pas' indicate curves for active and passive force, respectively.

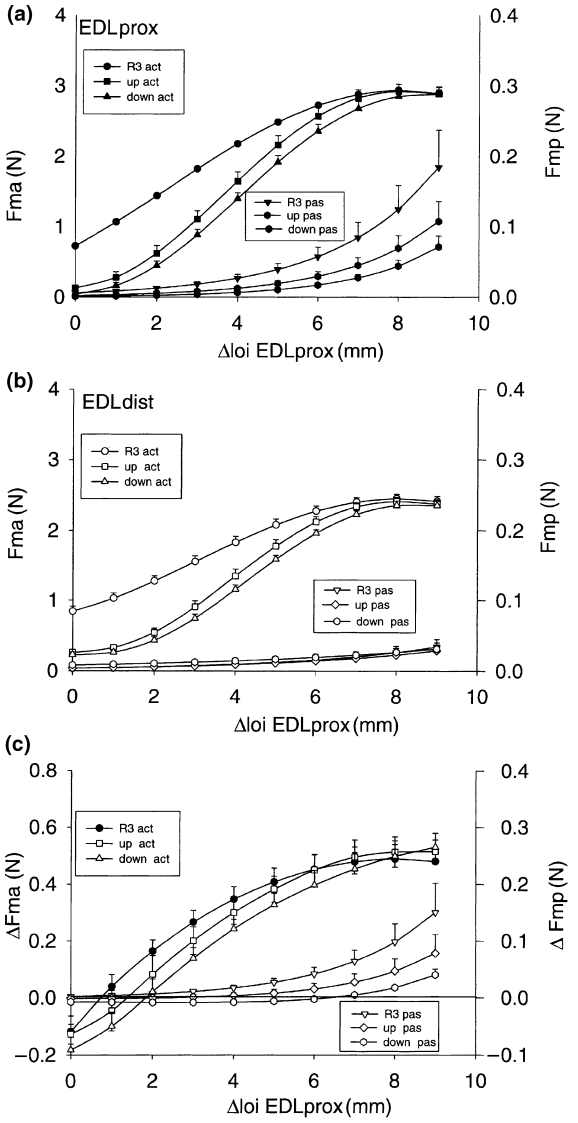

Figure 6 Effects of previous activity *at high lengths* and effects of length order on extensor digitorum longus (EDL) length–force characteristics and EDL proximo-distal force difference. Subsequent to the experiment of Figure 5, each target length was studied again at 2 min intervals once for increasing length order and once for decreasing length order. (a) Proximal active and passive EDL length–force characteristics. (b) Distal active and passive EDL length–force characteristics. (c) Difference between EDL proximal and distal force (active as well as passive) as a function of length. F_{ma} and F_{mp} represent active and passive force, respectively. Note that different axes are shown for active (left vertical axis) and passive forces (right vertical axis) or proximo-distal force differences, with quite different scaling factors. Mean results and standard errors of the mean ($n = 5$) are shown. For reference the last curve of the sequence shown in Figure 5 (indicated by R3) is included as well. 'act' and 'pas' indicate curves for active and passive force, respectively.

Length history dependence of EDL force and proximo-distal force difference

Active force. Both EDL length–distal force characteristics and length–proximal force characteristics were altered significantly after previous activity near optimum length (Fig. 6). Note that at the highest lengths studied, proximal as well as distal force is still quite reproducible. In contrast, for both proximal as well as distal EDL force (Fig. 6a, b) a very sizeable decrease of force was found specifically at lower lengths. For example at minimum length, mean active force decreased by 82.2% for proximal force and 69% for distal force, respectively. At most lengths, such changes are larger for proximal than for distal measurements of EDL force.

Therefore, it is concluded that isometric muscle activity at higher length substantially altered subsequent conditions of measurements at lower length, without affecting the high length properties themselves.

Despite such changes in both proximal and distal active EDL force, the proximo-distal active force difference is still present at a substantial magnitude (Fig. 6c), but the curve, describing this difference as a function of length, has become less curvilinear. This also caused a shift of cross-over length to higher length by approximately 0.5 mm (Fig. 6c).

Extensor digitorum longus length–force characteristics are influenced significantly also by the order of lengths imposed during measurements. Proximal and distal forces measured at reversed length order (high to low length: 1 mm decrements) were significantly lower (Fig. 6a, b): Distal force, as well as proximal force for the higher length range ($\Delta l > 3$ mm), by approximately 8–12%. However, the decrease in proximal force rapidly increased to approximately 50% with decreasing length. It should be noted that this is another differential effect for proximal and distal active force.

Despite these hysteresis and other effects, the proximo-distal EDL active force difference is again still present with a similar maximal range (Fig. 6c: ≈–0.3 to +0.45 N) for the decreasing length order measurements. However, a further decrease in the degree of curvilinearity is seen, accompanied by another shift of cross-over length (≈+0.5 mm).

Subsequently repeating the increasing length order determination of proximal and distal EDL length–active force characteristics (not shown), yielded very similar curves, i.e. no significant differences from the previous determination in that same length order. Therefore, the same applied for the proximo-distal EDL force difference. It is also concluded that an initial effect of activity at high length on force exerted subsequently at low length permanently modifies the active muscular characteristics or the duration of the present experiments.

Passive force. For EDL distal passive force no significant effects could be shown either after previous isometric activity at high lengths or by the decreasing length order of the measurements (Fig. 6b). In contrast (Fig. 6a), EDL proximal passive force after previous isometric activity at high lengths was decreased significantly (for example by 39% at the highest length studied). At high as well as lower lengths, significant decreases of proximal passive force were seen for the decreasing length order measurements with respect to the increasing ones However in any of the experimental conditions, proximal and distal passive force are not at similar levels (Fig. 6c), e.g. EDL proximal passive force measured after previous isometric activity at high lengths is maximally approximately 3.7 times higher than distal passive force.

It is concluded that, in any study involving multiple determinations of length–force characteristics, substantial length history effects on EDL length–force characteristics have to be taken into account, particularly for muscle embedded more or less in its natural connective tissue surroundings.

It is concluded that the presence of a length dependent proximo-distal EDL difference in active and passive force is a permanent feature. Although effects of length history affects the size of the proximo-distal EDL force difference at certain lengths, it certainly does not abolish such a difference in any of the conditions studied.

Proximal and distal forces in extensor digitorum longus after removal of tibialis anterior and extensor hallucis longus

After fully opening the anterior tibial compartment, all muscles, except EDL, were removed from the compartment, with the exception of a proximal part of TA near major neurovascular tracts within the compartment. An example of such a remaining tract is shown in Figure 4d (inset). Note that dissection removes most of the sheet (exposed in Fig. 4d), except for connective tissue immediately surrounding major nerves and blood vessels to EDL.

Length–force characteristics

Active. No significant differences or interaction between factors (length and location within the muscle) could be shown for proximal and distal active EDL forces after this isolation (Fig. 7a). It is concluded that isolating EDL from other muscles of the anterior tibial compartment removes any proximo-distal difference in active force.

Comparing active force levels per muscle at given length before and after the intervention of two groups of results can be distinguished on the basis of length effects. (1) At high muscle lengths, proximal and distal EDL force attained similar values because proximal EDL force is decreased to the level of distal EDL force, which itself was similar before and after removal of TA + EHL muscles. In one muscle only, proximal and distal EDL forces both decreased at higher lengths, yet to similar levels. (2) At lower lengths, both proximal and distal forces decreased to similar levels, i.e. proximal EDL force decreased more than distal EDL force by removing the other muscles from the compartment. Therefore it is concluded that the major change in force that removed proximo-distal differences for EDL force after removal of TA + EHL was a change in proximal force. At high EDL lengths, equality of proximal and distal active force was obtained by a decrease of proximal EDL force in response to isolating EDL from

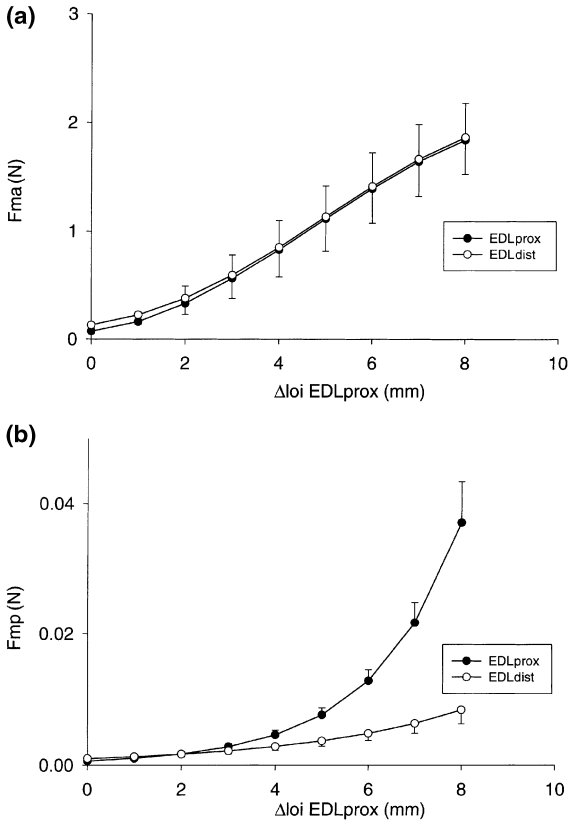

Figure 7 Extensor digitorum longus (EDL) length–force characteristics after isolation from most of the tibial compartmental connective tissue. (a) Active force exerted by EDL at its proximal and distal tendons. (b) Passive forces exerted by EDL at its proximal and distal tendons. F_{ma} and F_{mp} represent active and passive force, respectively. Mean results and standard errors of the mean ($n = 5$) are shown. Length changes of the EDL muscle tendon complex, imposed by moving the proximal force transducer, are expressed as deviations (Δl_{oi} EDL) from a minimal length (see Methods).

other muscles. At lower EDL lengths, both proximal and distal forces decreased in such a way as to obliterate the proximo-distal difference.

It should be noted that the combined effects of complete compartmental fasciotomy and isolating EDL from other muscles must have caused optimum length for both proximal and distal EDL forces to shift to higher muscle tendon complex lengths (compared with Fig. 3a). After the intervention, in a similar experimental length range, no optimum was encountered for either proximal or distal EDL force. Therefore optimum length is expected to be shifted to higher lengths. Similar results were found for active slack length: After removal of TA + EHL, at minimal length ($\Delta l = 0$) both proximal and distal active EDL force approaches zero levels, i.e. in contrast with initial conditions, EDL active slack length is almost brought into the window of the experimental length range. The combined results for active slack length and optimum length are indicative for a general decrease of sarcomere lengths for any given muscle length, as effect of isolating EDL from neighbouring muscles and most of the compartment. It is concluded that intact extra- and intramuscular connective tissue, is essential for extramuscular myofascial transmission of active force.

Passive. In contrast to results for active force, for most lengths studied, passive forces were still significantly higher for EDL force measured proximally than distally (Fig. 7b). Distal EDL passive forces were not very much affected by isolation of EDL from neighbouring muscles, and proximal EDL passive forces were decreased relative to their value before removal. Significant interaction between effects of length and location within the muscle was found as well. It is concluded that some extramuscular myofascial force transmission is still present for passive forces.

Morphology of remaining connections. The remaining proximo-distal difference of EDL passive force indicates that EDL is not fully isolated from surrounding tissues. As the neurovascular tract to EDL (Fig. 4d, inset) was not interfered with directly, the connective tissue of this tract, through which blood vessels and nerves reach EDL, is the most probable candidate for such a path of force transmission.

It is concluded that effects of extramuscular myofascial force transmission from the muscle through mechanical connections at the muscle belly are diminished (passive force) or fully removed (active force) by isolating EDL from most of the connective tissues and muscles of the anterior tibial compartment.

DISCUSSION

A major result of the present study is the almost permanent presence of a difference between proximally and distally exerted EDL forces (active as well as passive forces), as long as connective tissue of the anterior tibial compartment is intact at the level of the muscle bellies. Prior to the present study, on the basis of experimental result regarding intramuscular force transmission within EDL, we could only make inferences about the possibility of force transmission from the muscle by paths different from myotendinous ones (Huijing *et al.* 1998, Huijing 1999a, b). Despite a plethora of experimental work on humans and experimental animals *in vivo*, relatively little evidence indicative of any form of extramuscular myofascial force transmission can be found in literature. Wicke & Zajac (1981) reported, exclusively in an abstract, that at the cat ankle, a moment was produced on stimulation of semitendinosus and posterior biceps muscles by force transmission via the interconnecting fascial sheath. In a

dissection study on human cadavers, Vleeming *et al.* (1995) described a possibility for mechanical interaction gluteus maximus muscle with spinal muscles via the thoracolumbar fascia. In other species there are some indications that similar effects may play a role. It has been proposed (Vleeming *et al.* 1995) that these muscles are coupled mechanically and functionally, especially during the rotation of the trunk. If this is true *in vivo*, the combined action of these muscles would assist in rotating the trunk, while simultaneously stabilizing the lower lumbar spine and sacroiliac joints.

To the best of our knowledge, the present study is the first systematic study to argue that a proximo-distal force difference should be present and to quantify it, thereby yielding direct evidence for myofascial transmission of force from muscle.

For a description of our present experimental conditions as well as the *in vivo* situation, connections of the intramuscular connective tissue need to be taken into account. If the tensile or shear stiffness of intra to extramuscular connections is high enough, force may be transmitted through such connections in two major ways:

(i) From the intramuscular connective tissue via extramuscular connective tissue directly to bone (extramuscular myofascial force transmission);
(ii) Intermuscular myofascial force transmission (i.e. direct transmission from the intramuscular connective tissue of one muscle to that of the other).

Both paths could lead to differences in force measured at proximal and distal tendons, for which substantial indications were encountered in the present work (e.g. Figs 3 and 6c). The results indicate unequivocally that, for the experimental conditions imposed, connections of the EDL muscle belly to surrounding structures within the anterior tibial compartment (e.g. Fig. 4) play a major role in determining muscle characteristics. Our present results and some previous ones (Huijing *et al.* 1998, Huijing & Baan 2001) are compatible with a major fraction of the force being borne by the extracellular matrix. Therefore, previous views that the endomysial and/or perimysial systems are too compliant and cannot normally transmit active or passive force (e.g. Magid & Law 1985, Purslow & Duance 1990) do not seem tenable. However, a more recent view that, despite a higher compliance of the perimysium (e.g. Purslow 1999), force transmission is feasible, is compatible with our present findings.

Some determinants of the proximo-distal force difference

Length and relative position of a muscle. It is clear that actual length of a muscle has a decisive influence on this difference. For the present work, this change of isometric length has been obtained by proximal lengthening only. It is expected that distal lengthening of EDL will have similar effects, but will favour distal force, with consequences for the sign of the force difference. Therefore, it seems that it is not only the length of a muscle, but also its relative position or that of parts of it with respect to their surroundings that will affect the sign and size of the force difference. The differences in the time trajectories of the contraction seen at some EDL lengths (Fig. 2) may be a reflection of effects of differential lengths of proximal and distal segments of EDL. Some other differential results related to reproducibility and length history effects may also be related to different lengths of connective tissues and/or sarcomeres. In general, the effects of moving joints at either the distal or proximal end of a muscle are considered as similar in nature and additive (e.g. Grieve *et al.* 1978, Visser *et al.* 1990). For an isolated muscle that may be true, e.g. changing the length of a muscle by a given amount by pulling on its distal or proximal tendon will yield similar results. Because of extra- or intermuscular myofascial force transmission, this is not likely to be true *in vivo*. This means that, for monoarticular muscle but particularly for a muscle that spans more than one joint, movement of a proximal joint may lead to quite different muscular properties than moving a distal joint, despite similar changes of muscle length.

Viscous and plastic deformation. The size of the proximo-distal difference in EDL force is influenced also by effects that must be related to plastic and viscous deformation of the extracellular matrix, such as effects of previous activity at high length and hysteresis effects of experimental active length order (e.g. Fig. 6). However in either case, the actual presence of the proximo-distal force difference, and thus extramuscular myofascial force transmission, is not dependent on such effects, although the nature of its length dependence is affected by it (Fig. 6). Our results allow only speculations about the exact mechanisms by which the size of the proximo-distal force difference as well as the length–force characteristics are affected. But, a conceivable mechanism could be related to the effects of fluid flow through the extracellular matrix or movement of collagen with respect to more fluid parts of the extracellular matrix.

Interaction of extra- and intramuscular connective tissue

Previously, effects on length–force characteristics, ascribable to full fasciotomy of the anterior tibial compartment were studied exclusively for forces exer-

ted at one tendon (Garfin *et al.* 1981, Huijing & Baan 2001). For rat the anterior tibial compartment force at the proximal EDL tendon was studied (Huijing & Baan 2001). Those effects on proximal EDL length–force characteristics can be summarised by two types of changes in the length–force curve:
(i) Substantial decrease of active force at high length accompanied by a substantial increase of optimum length; (ii) A substantial increase of active force at low lengths, accompanied by a major shift of active slack length to lower length.

Such results are compatible with increased distributions of fibre and sarcomere lengths within EDL. The almost complete removal of TA and EHL yielded generally decreased active proximal EDL forces without further major changes in the shape and length range of the length–force curve (Huijing & Baan 2001).

In our present work, full lateral fasciotomy and removal of TA and EHL muscle were combined in one intervention. The inferred shift of EDL optimum lengths to higher lengths, after the intervention, as well as a general decrease in force (compare Figs 3 and 7) are in accordance with our previous results (Huijing & Baan 2001). However, the shift of active slack length to lower lengths, found in that previous work, is absent presently. The explanation for this difference is not immediately apparent, but may be related to the fact that for the one tendon study the whole anterior tibial compartment was fully intact, whereas it had to be opened distally in the present work.

Intermuscular force transmission?

In our present results we could find no unequivocal evidence that force is transmitted directly between adjacent muscles, as TA + EHL force could not be shown to be influenced significantly by changing EDL length and proximal position. In ongoing work (for a preliminary report see Maas *et al.* 2001), we did find indications for intermuscular transmission of force between EDL and TA + EHL. The magnitude and sign of the proximo-distal force difference in EDL at constant length, is very dependent on the length of TA + EHL. A potential explanation for the lack of effect in the present work could be the choice of length of this complex in our present work.

Some implications of inter- and extramuscular myofascial force transmission

We have to address the likelihood that such transmission will generally be quantitatively important. The anterior tibial compartment of mammals is a relatively stiff compartment, probably because of the relatively high contribution of bony parts (i.e. tibia and fibula) to its walls. This is also apparent from a relatively high incidence of compartment syndrome for this compartment in humans. However, the organization in different compartments leads to expectations that similar phenomena will also play a role in other compartments.

Muscle as an independent unit of function?. The presence of any proximo-distal force difference, and extramuscular myofascial force transmission of substantial magnitude, indicates for the muscle in question that it is not an independent mechanical unit. This could possibly be conceived as a self-evident statement, without much consequence. It should be realised, however, that the consequences of such dependence of muscular properties and function on its surrounding tissues are likely to profoundly affect our thinking about muscular function, as well as our research efforts.

Extramuscular myofascial force transmission and adaptation. Recent views on adaptation of muscle are shifting to a possibility of direct mechanical deformation of the cell nuclei (Wang *et al.* 1993, Ingber 1997) in addition to biochemical trans-membrane signalling. Even autocrine muscular activity (Goldspink 1999) may be related to processes of myofascial force transmission, as these pathways could conceivably be active as a path in exerting direct effects from a whole compartment onto nuclei within muscle fibres and fibrocytes of muscle.

Work on isolated single muscle fibres has been performed since a little more than half a century (e.g. Ramsey & Street 1940, Gordon *et al.* 1966a,b). That type of work is very necessary for studying the molecular and supramolecular mechanisms active in muscle fibres. The presence of myofascial force transmission much complicates the study of such mechanisms even in whole isolated muscles. However, it should be realised, that in an isolated muscle fibre, major influences of intramuscular (Huijing *et al.* 1998) and extramuscular myofascial force transmission are removed. Therefore extrapolation particularly of results on mechanics of isolated muscle fibres to isolated whole muscle or *in vivo* conditions should take into account any effects of myofascial force transmission.

The present work indicates that, *in vivo*, a sizeable fraction of muscular force may be exerted on compartmental connective tissues. It is likely that such extramuscular forces and possibly also intermuscular forces and their accompanying deformations will play a

major role in the aetiology of afflictions of the human locomotion apparatus such as repetitive strain injury, tennis elbow, musicians arm, etc.

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